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The Cebines

Toward an Explanation of Variable Social Structure

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1. While the cebines are widely distributed throughout Central and South America, only members of the genus *Cebus* appear to be able to exploit variable habitat types (they are referred to as "habitat generalists"). What characteristics (e.g., behavioral, morphological, social) enable *Cebus* to occupy diverse habitat types, and what characteristics act to restrict *Saimiri* to mainly secondary lowland tropical rain forests?
2. What is parallel dispersal, and how does it affect the social relationships of the cebines?
3. As a genus, *Saimiri* are unique in that they display a full range of dispersal patterns observed in group-living primates. What are these patterns, and why do we see such diversity across this genus?

INTRODUCTION

Capuchins (genus *Cebus*) and squirrel monkeys (genus *Saimiri*), which together make up the subfamily Cebinae, are among the most widely recognized species of New World primates. Some may recognize capuchins as the hat-tipping, money-collecting partner of the organ grinder or may have seen them in movies or television ads spreading a deadly strain of the Ebola virus or as the "spokesperson" for any number of products, both of which have little to do with being a capuchin or a primate. Although perhaps not quite as recognizable as their capuchin cousins, squirrel monkeys are also well known because of their prominence in the illegal pet trade and their use in biomedical research; they are one of the most commonly used laboratory primates, second only to rhesus macaques (*Macaca mulatta*) (Kinzey 1997c). Although these two primate genera have much in common and can often be observed in the same forests in Central and South America, they comprise a very diverse subfamily, particularly in respect to their morphology and behavioral ecology.

TAXONOMY AND DISTRIBUTION

The taxonomic classification of the platyrrhines has seen a long history of debate, and the exact placement of the genera *Cebus* and *Saimiri* within the infraorder has been particularly problematic (see Janson and Boinski 1992 for

review). Ford and Davis (1992:434) sum the problem up succinctly, stating that "*Cebus* and *Saimiri* are in some ways enigmatic" and "[t]heir potential relationships to each other and to other New World monkeys remain unclear" (see also Tyler 1991). They argue that morphological and life history data indicate that *Cebus* may have separated from the other platyrrhines as many as 20 million years ago and, accordingly, they should be placed within their own subfamily. Groves (2001a) agrees, placing *Cebus* in the subfamily Cebinae and *Saimiri* in Chrysotrichinae (also Saimirinae; see Rosenberger's interpretation in Schneider and Rosenberger 1996), although he does group these two neotropical primates together in the family Cebidae, accompanied only by the small squirrel-like marmosets and tamarins (*Callithrix*, *Callimico*, *Leontopithecus*, and *Saguinus*; subfamily Hapalinae). Contrary to these classification schemes that place *Cebus* and *Saimiri* in different subfamilies, other taxonomists argue that current phylogenetic analyses of both morphological and molecular data support the placement of these two genera together within the Cebinae subfamily (Schneider et al. 1993; for recent reviews, see Rylands et al. 2000 and Schneider and Rosenberger 1996). The question of whether or not the marmosets and tamarins, and perhaps owl monkeys (*Aotus*), should accompany *Cebus* and *Saimiri* in the Cebinae subfamily is still highly debated; and here I follow Rylands et al. (2000) in considering *Cebus* and *Saimiri* to be the exclusive members of Cebinae and use the term "cebine" to refer solely to these two genera.

Four species of *Cebus* (*C. apella*, *C. albifrons*, *C. capucinus*, and *C. olivaceus*) and more than 30 subspecies are traditionally recognized (Ford and Hobbs 1996). A fifth species, *C. kaapori*, discovered in 1992 (Queiroz 1992, cf. Masterson 1995), is increasingly included in this list. Groves (2001a) and Rylands et al. (2000) have called for the recognition of *C. libidinosus*, *C. xanthosternos*, and *C. nigrinus* as distinct species rather than subspecies of *C. apella*, as they have previously been classified (see Fragaszy et al. 2004b for review). The four better-known *Cebus* species are divided into two main groups according to the presence or absence of tufts on the top of the head. The tufted group contains only one species, *C. apella*, while the untufted group contains *C. albifrons*, *C. capucinus*, and *C. olivaceus* (Hershkovitz 1949 based on Elliot 1913).

The number of species included within the genus *Saimiri* has been widely investigated, and molecular studies conducted in the last decade have shed much light on the topic. Historically, the genus was divided into only two species based on geographic distribution: *S. oerstedii* in Central America and *S. sciureus* in South America. In some accounts, *S. oerstedii* is listed as an offshoot of *S. sciureus* that was thought to have been introduced to Central America by humans in pre-Columbian times (Hershkovitz 1969; cf. Cropp and Boinski 2000, Costello et al. 1993; see Boinski 1999 for review of *Saimiri* taxonomy); however, genetic analyses have shown this not to be the case, and it is now known to be a distinct species (Cropp and Boinski 2000). Taxonomists are now in general agreement on the division of *Saimiri* into five species, with as many as 12 subspecies: *S. oerstedii*, *S. sciureus*, *S. boliviensis*, *S. ustus*, and *S. vanzolinii* (Groves 2001a, Rylands et al. 2000). This division is based on a variety of molecular, morphological, and behavioral data (Boinski and Cropp 1999; see also Ayres 1985, Groves 2001a). It should be noted that the previous practice of classifying all South American squirrel monkeys together as *S. sciureus* does lead to some confusion when trying to decipher early reports of squirrel monkey taxonomy and behavior. In particular, most of our current information on *S. boliviensis* comes from Mitchell's (e.g., 1990) study at Manu, Peru, where the species was formerly referred to as *S. sciureus* (see Boinski 1999). The species designator "sciureus" is now reserved for squirrel monkey populations in the northeastern Amazon Basin (Colombia, Ecuador, and Venezuela) and the Guyana Shield (Boinski 1999, Boinski and Cropp 1999).

The geographic distribution of the cebines overlaps extensively; indeed, the two genera are often found in sympatry and commonly form mixed-species associations (see later section "Ecology"). The geographic range of *Cebus* is more extensive than that of *Saimiri* and, among New World monkeys, is second only to that of *Alouatta* (howler monkeys) (Sussman 2000). *Cebus* range throughout much of Central and South America, from Honduras in the north to Argentina in the south (Eisenberg 1989) (see

Fig. 8.1 for map of *Cebus* distribution). With the exception of *C. capucinus*, which ranges from Honduras through the northwestern coast of Ecuador (Rowe 1996), all *Cebus* species are indigenous to South America (see Table 8.1 for species distributions and common names). Despite the large geographic distribution of this genus, long-term field studies have been limited, with the majority of data coming from six main field sites: *C. capucinus* in Santa Rosa and Lomas Barbudal (Costa Rica); *C. olivaceus* in Hato Masaguaral (Venezuela); and *C. apella* in Iguazu (Argentina), Manu (Peru), and a study begun in 2000 at Raleighvallen (Suriname) (see Fragaszy et al. 2004b for a complete overview of field studies of *Cebus*). To date, only short-term studies of *C. albifrons* have been undertaken in Peru (Janson 1984, 1986), Colombia (Defler 1979a,b, 1982), Ecuador (Field 2008, Matthews 2008, Jack 2005), and Trinidad (Phillips and Abercrombi 2003). Despite this apparent paucity of studies focused on this genus in the wild, particularly in comparison to the long-term field studies of many Old World monkey and ape species, *Cebus* is one of the most extensively studied genera of New World primates, with studies of *C. capucinus* in Costa Rica well into their third decade.

Saimiri are found in two geographically separated pockets. A single species, *S. oerstedii*, is isolated in Central America in a relatively small area of lowland forests that extend from the central Pacific coastline of Costa Rica through the Pacific Coast of western Panama. The remaining

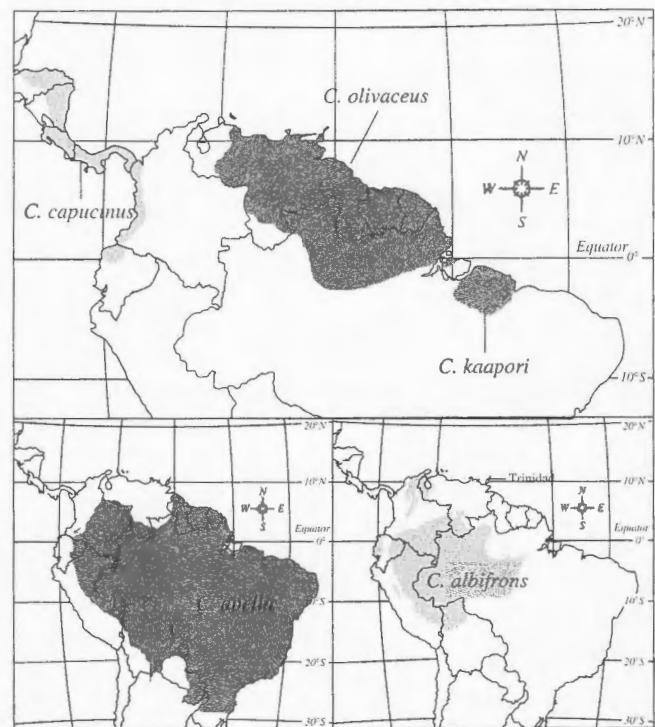


Figure 8.1 Distribution map of *Cebus* (B. Lenz, adapted from Fragaszy et al. 2004a).

species occur in the lowland forests of the Amazon Basin of South America from Guyana through Paraguay (Boinski et al. 2002) (Fig. 8.2 and Table 8.1). To date, long-term studies of *Saimiri* have been limited: *S. oerstedii* in Corcovado, Costa Rica (e.g., Boinski 1987c, 1988a); *S. boliviensis* in Manu, Peru (Mitchell 1990, 1994; Boinski 1991, 1994); and *S. sciureus* in Raleighvallen, Suriname (Boinski 1999), which is currently the only long-term investigation being undertaken on this genus (see Boinski et al. 2002 for a summary of shorter studies).

ECOLOGY

Morphological Adaptations to Habitat and Diet

Cebus are medium-sized primates, with females weighing 1.4–3.4 kg (mean = 2.3 kg) and males ranging 1.3–4.8 kg (mean = 3.0 kg) depending on the species under consideration (see Table 8.2). *Cebus* display moderate levels of sexual dimorphism, with males weighing 19.5%–27% more than females (mean = 24%, Table 8.2) and possessing canine teeth that are 16%–22% larger than female canines (Kay et al. 1988). *Saimiri* are considerably smaller than *Cebus*, with male weights ranging 620–1,200 g (mean = 884 g) and female weights ranging 600–880 g (mean = 700 g). However, the degree of sexual dimorphism in body size is comparable across the two genera (male *Saimiri* are on average 19.7% larger than females) (Table 8.2) (see also Janson 1984). Both *Cebus* and *Saimiri* show large brain

to body weight ratios, particularly for primates of their size, a trend that may be an adaptation to their relatively large home ranges, variable diets (Stephen et al. 1988; see Terborgh 1983 for home range comparisons), and/or complex

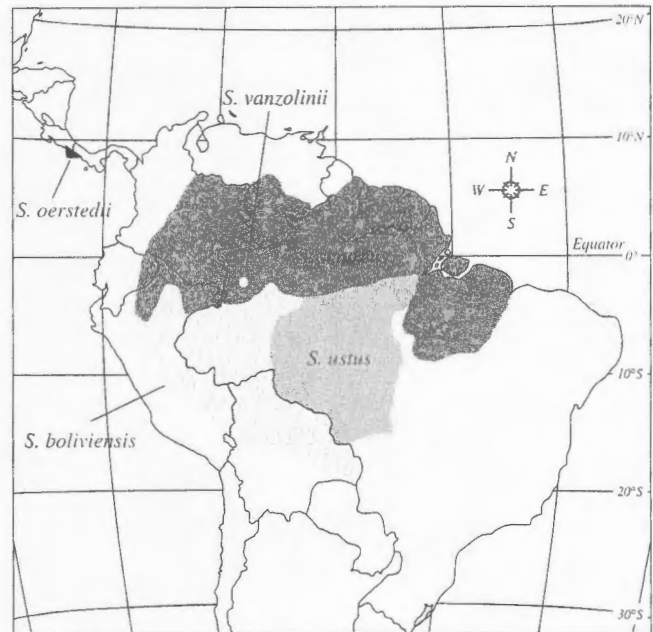


Figure 8.2 Distribution map of *Saimiri* (B. Lenz, adapted from Boinski 1999).

Table 8.1 Species, Common Names, and Geographic Distribution of the Most Commonly Recognized Cebines

SCIENTIFIC NAME	COMMON NAME	GEOGRAPHIC DISTRIBUTION
<i>Cebus albifrons</i>	White-fronted capuchin	Brazil, Colombia, Ecuador, Peru, Venezuela, northern Bolivia, and Trinidad
<i>C. apella</i> ¹	Tufted, black-capped, or brown capuchin	Northern and central South America from Colombia and Ecuador (west of the Andes) through coastal Brazil
<i>C. capucinus</i>	White-faced, white-headed, or white-throated capuchin	Honduras through northwestern Ecuador
<i>C. olivaceus</i> (also <i>C. nigrivittatus</i>)	Weeper or wedge-capped capuchin	Northeastern Brazil, Guyana, French Guiana, Suriname, and Venezuela
<i>C. kaapori</i>	Ka'apor capuchin	Brazil
<i>Saimiri oerstedii</i>	Red-backed or Central American squirrel monkey	Central Pacific Coast of Costa Rica through Pacific Coast of Panama
<i>S. sciureus</i>	Common or South American squirrel monkey	North-central South America (Brazil, Guyana, French Guiana, Suriname, Venezuela, Ecuador, and Colombia)
<i>S. ustus</i>	Golden-backed or bare-eared squirrel monkey	Northwestern Brazil
<i>S. boliviensis</i>	Bolivian or black-capped squirrel monkey	Brazil, Bolivia, Peru
<i>S. vanzolinii</i>	Black squirrel monkey, many classify with <i>S. ustus</i>	Northwestern Brazil

¹ *C. libidinosus*, *C. xanthosternos*, and *C. nigrinus* are now considered by many taxonomists to be distinct species, rather than subspecies of *C. apella*. The above list follows more traditional taxonomy.

Sources: *Cebus*, Groves 2001a, Rowe 1996, Fragaszy et al. 2004b; *Saimiri*, Groves 2001a, Boinski 1999, Rowe 1996.

Table 8.2 Adult Weights and Sexual Dimorphism of the Cebines

GENUS	SPECIES	MALE BODY WEIGHT RANGE (MEAN) (G)	FEMALE BODY WEIGHT RANGE (MEAN) (G)	DEGREE OF SEXUAL DIMORPHISM
<i>Cebus</i>	<i>albifrons</i>	1,700–3,260 (2,480)	1,400–2,228 (1,814)	27%
	<i>apella</i>	1,350–4,800 (3,050)	1,758–3,400 (2,385)	22%
	<i>capucinus</i>	3,765–3,970 (3,668)	2,610–2,722 (2,666)	27%
	<i>olivaceus</i>	1,447–4,500 (2,974)	1,589–3,200 (2,395)	19.5%
Mean		3,043	2,315	24%
<i>Saimiri</i>	<i>boliviensis</i>	(992)	(751)	24.3%
	<i>oerstedii</i>	750–950 (829)	600–800 (695)	16%
	<i>sciureus</i>	(740)	(635)	14%
	<i>ustus</i>	620–1,200 (910)	710–880 (795)	13%
	<i>vanzolinii</i>	(950)	(650)	31.5%
Mean		884	705	19.7%

Sources: Ford and Davis 1992 (data based on wild individuals only). Boinski (1999); with the exception of those weights for female *S. oerstedii*, sexual dimorphism for *S. boliviensis*, male *S. oerstedii*, and *S. sciureus* has been calculated based on weights provided in Boinski (1999) rather than Ford and Davis (1992) because of earlier practices of lumping numerous species under *S. sciureus*.

foraging patterns (e.g., Fragaszy 1990, Parker and Gibson 1977, Terborgh 1983).

In addition to differences in absolute body size, *Cebus* and *Saimiri* display considerable morphological variability. For example, although both genera have skeletons adapted for quadrupedal locomotion, they differ markedly in their relative limb proportions. Unlike other platyrrhines, *Cebus* tend to have forelimbs and hindlimbs of fairly equal proportions, while *Saimiri* have comparatively longer hindlimbs (Fleagle 1999). This is likely an adaptation for the more frequent leaping that characterizes *Saimiri* locomotion, while the equal limb lengths of capuchins may be an adaptation for their more terrestrial locomotor patterns (Janson and Boinski 1992). Overall, *Cebus* postcranial anatomy is more similar to that of terrestrial Old World monkeys than it is to that of other platyrrhines, which is likely because capuchins, particularly the untufted species, spend more time on the ground than other platyrrhines. Capuchins also have a semiprehensile tail that, unlike their ateline cousins (see Chapter 11), is fully covered in fur and unable to sustain the full weight of an adult. Instead, the tail provides support and balance and is commonly used to anchor an individual to trees while foraging (see Fig. 8.3). Squirrel monkeys locomote quadrupedally along the surfaces of thin branches and lianas, often leap between them (Boinski et al. 2002), and rarely descend to the ground to forage. Although they are born with prehensile tails, the grasping ability is lost with age and the rather large tail of adults assists only in balance (Boinski 1989a) (Fig. 8.4).

The dentition of *Cebus* and *Saimiri* is also variable and appears to reflect dietary differences between the two genera. Although cebines are considered the most omnivorous

of the platyrrhines (Fleagle 1999) and both *Cebus* and *Saimiri* are traditionally categorized as frugivore–insectivores (Robinson and Janson 1987), *Saimiri* display a relatively heavier reliance on insects, while *Cebus* rely more on fruit (see Janson and Boinski 1992 for review). The cebines spend upward of 75% of their day engaged in active foraging (Robinson and Janson 1987), and *Saimiri* can spend up to 80% of this time foraging just for insects. The diets of both genera are extremely flexible, and individuals are able to alter their diet to become very specialized in response to changing environmental conditions. For example, during the peak of the dry season, *Saimiri* are able to become complete insectivores for up to a week at a time, while *Cebus*, which can survive in very marginal habitats, can rely almost completely on bromeliads (a plant in the family that includes pineapples) or become seed predators in times of food stress (see Sussman 2000 for review). *Cebus* are very adept at capturing small vertebrate prey, including birds (and eggs), lizards, squirrels (Fig. 8.5), and coatis, although such animal prey form only a small portion of their diet (~0.5%–2.5%) (Sussman 2000). The hunting behavior displayed by *Cebus* is opportunistic rather than cooperative in nature (see Perry and Rose 1994). Interestingly, at least among *C. capucinus*, the individual that captures the prey, regardless of age or sex class, is able to eat it with only minimal harassment from other group members (K. M. Jack personal observation). Although food sharing does occur in this genus, it is indirect in that bits of food are dropped or left behind for other group members to eat (Perry and Rose 1994).

Cebus are often referred to as “habitat generalists” (Chapman et al. 1989a) in that they occupy a great



Figure 8.3 An adult male *Cebus capucinus* using his semiprehensile tail to anchor him while foraging for insects (photo by Katharine M. Jack).



Figure 8.4 An adult female *Saimiri oerstedii* with 6-month-old infant. Note the lack of prehensile tails (photo by Katharine M. Jack).

diversity of habitats, including primary forests of all types (rain, cloud, dry, deciduous, etc.), highly disturbed and fragmented areas, as well as swamp and seasonally flooded forests (Freese and Oppenheimer 1981). Members

of the genus *Cebus* are the most dextrous of the platyrrhine primates. They have shortened fingers, “pseudo-opposable thumbs,” and the ability to move all digits independently of the others (Janson and Boinski 1992). This dexterity, accompanied by what seems to be an innate curiosity, is readily visible in their foraging habits. Capuchins are extractive foragers (Parker and Gibson 1977) and appear to specialize in consuming foods that “fight back”—foods that have hard protective coverings, toxins, and other predatory defenses or insects and vertebrates that bite and/or sting (Fragaszy et al. 2004b). In order to access these foods, wild capuchins will pound hard husked or shelled objects onto a substrate, and they frequently rid food items of spines or poisonous hairs by rubbing them against branches (Panger et al. 2002b). In some cases, these food items are wrapped in leaves prior to rubbing, perhaps as a way of directly protecting the hands from the toxins they are attempting to remove (Panger et al. 2002b). Fragaszy et al. (2004a) recently described a wild group of *C. apella* in Brazil that are regularly observed to crack open palm nuts using rocks in a hammer and anvil-type fashion, further demonstrating the dexterity and ingenuity of these small New World primates. Capuchins have been observed using a variety of other tools in the wild, including a club to attack a venomous snake, leaves as containers, and probing tools to access imbedded foods; among the nonhuman primates, capuchins and the great apes are considered to be the most adept and varied tool users (see Panger et al. 2002b). Another characteristic that *Cebus* has evolved as a means of gaining access to protected foods (e.g., palm nuts) is their thick tooth enamel; in fact, when tooth size is



Figure 8.5 An adult male *Cebus capucinus* holds a young squirrel he has just killed (photo by Katharine M. Jack).

taken into account, *Cebus* show the thickest tooth enamel of any nonhuman primate (Kay 1981; see Janson and Boinski 1992 for review).

Despite their large geographic distribution, the habitat preferences of *Saimiri* show extreme ecological consistency (see Janson and Boinski 1992). *Saimiri* show a preference for tropical lowland rain forests (Boinski et al. 2002), with most activities concentrated in secondary forests and relatively little time in primary and late successional forests (Boinski 1987c; see Sussman 2000 for review). Although, in general, the cebines are more manually dextrous than other platyrrhines, *Saimiri* do not possess the manipulative abilities that are so characteristic of capuchins. Squirrel monkeys do not have independently mobile digits, nor do they possess opposable thumbs, a combination that prohibits them from generating a strong grip between the fingers and thumb (Janson and Boinski 1992). Although both *Saimiri* and *Cebus* rarely go after prey that is in motion, *Saimiri* are more prone to hunt potentially mobile prey that are visible on substrate surfaces (branches, leaves, tree trunks) than are *Cebus*. Squirrel monkeys also specialize in finding insects by unrolling both dead and living leaves to reveal invertebrate prey imbedded within them (Fig. 8.6) (Janson and Boinski 1992).



Figure 8.6 An adult male *Saimiri boliviensis* unrolling a dead leaf in search of imbedded invertebrate prey (photo by B. Lenz).

Predation: Susceptibility and Behavioral Adaptations

Both *Cebus* and *Saimiri* are at risk of being taken by similar types of predators, including raptors, felids, constricting and venomous snakes, coyotes, and tayras (an arboreal mammal that is part of the weasel family, *Mustelidae*) (Freese 1983, van Schaik and van Hooff 1983, Terborgh 1983, Chapman 1986, Boinski et al. 2002, Bianchi and Mendes 2007). However, given that an adult capuchin outweighs an adult squirrel monkey by as much as seven times, it is not surprising that *Saimiri* are much more susceptible to predation than are *Cebus* (Fedigan et al. 1996). Raptors are the main predators observed to kill *Saimiri*, and Boinski (1987b) reports that 50% of all infants born to *S. oerstedii* do not survive to 6 months of age due to confirmed or suspected predation by avian predators. Boinski et al. (2002) report similar predation rates on *S. boliviensis*, while *S. sciureus* of Suriname appear to be at lower risk despite an intact predator community. Perhaps as a response to their susceptibility to predation, *Saimiri* form groups that are usually between three and six times the size of *Cebus* troops (see later section "Social Organization"); and although both genera are known for being highly vocal primates that display a great repertoire of call types, *Saimiri* have more calls that serve as contact calls than do *Cebus*. While these vocalizations do not directly function in predator avoidance or detection, they are believed to function as a type of "security blanket," to make up for the visual separation that occurs while squirrel monkeys forage and enable group members to keep

alerted to the presence and location of their group mates (see Fedigan et al. 1996 for review).

The South American populations of *Saimiri* have developed another way of combating their high risk of predation: In all areas where they occur sympatrically, *Saimiri* parasitize on the predator-detecting abilities of *Cebus* by joining them in their daily activities (Waser 1987). These mixed-species associations may last several days, and for the most part the two genera will interact peacefully. However, it is not uncommon for an adult male capuchin to chase away an entire group of squirrel monkeys, although the displaced squirrel monkeys usually quickly return to their capuchin comrades. Data from South American cebine populations, particularly those coming from Manu, Peru (e.g., Terborgh 1983, Terborgh and Janson 1986), have shown that it is *Saimiri* rather than *Cebus* that maintain these mixed-species associations. Terborgh (1983) reports that, in Manu, *Saimiri* actually seek out *Cebus* and that although *Saimiri* often appear to be leading the movements and direction of the mixed-species foraging excursions, they will usually backtrack if the capuchins lag behind or fail to follow them. The maintenance of these associations with capuchins is thought to benefit squirrel monkeys in terms of both increased foraging efficiency and predation avoidance. For example, when they are not in association with *Cebus*, squirrel monkeys travel twice as far in an hour. They also appear to benefit from the more detailed knowledge that *Cebus* have of fruiting tree locations during times of resource scarcity. In addition, *Saimiri* gain access to fruits dropped by *Cebus* that they would otherwise be unable to open (e.g., tough-husked palm nuts). Despite the obvious foraging advantages that these associations provide, the real advantage for *Saimiri* seems to lie in the increased predator-detection skills of *Cebus* (Terborgh 1983; see also Sussman 2000 for review). *Saimiri* appear to benefit greatly from the ever-vigilant capuchin males and the alarm calls that they emit; in fact, squirrel monkeys respond more readily to *Cebus* alarm calls than they do to the alarm calls of their own group members (Terborgh 1983). *Cebus*, on the other hand, do not seem to benefit much from these associations; they pay little attention to *Saimiri* alarm calls, and they travel up to 40% more when in the company of squirrel monkeys. It is no wonder, then, that capuchins do not wait for sidetracked squirrel monkeys to catch up when they lag behind.

Interestingly, in Central America, sympatrically occurring *Cebus* and *Saimiri* do not form mixed-species associations more frequently than predicated by chance. Given that *S. oerstedii* are under severe predation pressure, particularly from raptors (Boinski 1987b), would they not also benefit from the predator-detection skills of *C. capucinus*? Boinski (1989b) reports that in Corcovado National Park, Costa Rica, the two cebine genera spent only approximately 6% of their time in association with one another, which greatly contrasts with the 90% rate reported for *S. boliviensis* with *C. apella* and *C. albifrons* in Peru. Boinski (1989b) suggests

that the two Central American species do not form mixed troops simply because the presence of *C. capucinus* would impose very high foraging costs on *S. oerstedii*. Her study showed that *Saimiri* would have little to gain by associating with *Cebus* even in terms of increased predator detection and avoidance. Boinski concluded that, although *Cebus* in Costa Rica are susceptible to predation, their vigilance does not appear to function for detecting predators. Several studies focusing on male vigilance in *C. capucinus* have shown that while they are alert to potential predators, as evidenced by their elaborate alarm calls that differ according to predator types, the majority of their vigilance is directed at detecting extragroup males (Rose and Fedigan 1995) or monitoring the activities of their coresident males (Jack 2001). The foraging costs and limited benefits associated with detecting predators appear to have precluded the formation of mixed-species groups between the Costa Rican celines, although this topic requires further detailed investigation.

REPRODUCTIVE PARAMETERS

Saimiri are highly seasonal breeders, with all matings being confined to an annual 2-month period and births being even more tightly synchronized (Table 8.3). For example, *S. oerstedii* are reported to have the most restricted birth season of any primate species, with group females giving birth within the same 1-week period (Kinzey 1997c, Boinski 1987b). *C. apella* in Argentina is the only capuchin population studied thus far that displays a true birth season, which in turn reflects mating seasonality (Di Bitetti and Janson 2000, 2001a). While the other *Cebus* species do show a yearly birth peak during which the majority of infants are born, they are not strict seasonal breeders as births occur throughout all months of the year (Freese and Oppenheimer 1981, Robinson and Janson 1987, Fedigan and Rose 1995). Like most New World monkeys, cebine birth peaks or seasons generally coincide with seasonal peaks in resource availability (Di Bitetti and Janson 2000). *Cebus* interbirth intervals range 18–26.4 months (mean = 22 months), while *Saimiri* interbirth intervals, with the exception of *S. boliviensis* where females give birth every other year, tend to be shorter and average 12 months (see Table 8.3).

Compared with other mammals, where life history variables strongly correlate with body size, primates show very long life histories, particularly in their tendency toward extreme delays in reproductive maturity (Promislow and Harvey 1990, Purvis et al. 2003). If we restrict the examination of life history variables and body size to the order Primates, the general pattern holds, with larger primates showing slower life histories than smaller ones (Eisenberg 1979). However, comparing published data available for New World species, *Cebus* do not fit this general pattern. Rather, their maturation rates and overall life history variables are more comparable with members of the subfamily

Table 8.3 Cebine Reproductive Parameters and Life History Variables

GENUS	SPECIES	BIRTH SEASON	INTERBIRTH INTERVAL (MONTHS)	FEMALE AT FIRST BIRTH (YEARS)	MALE ADULT SIZE, REPRODUCTIVE MATURITY (YEARS)	LIFE SPAN (CAPTIVE)
<i>Cebus</i>	<i>albifrons</i>	Peak ¹	18 ³	N/A	N/A	44 ¹⁵
	<i>apella</i>	Peak-Peru				
		Season-Argentina ¹	19.4 ⁴	7 (wild) ¹	7 ^{11,12} , 4.5 ¹ (captive)	45.1 ¹⁵
	<i>capucinus</i>	Peak ¹	26.4 ⁵	7 (wild) ¹	10 (wild) ¹³	54.8 ¹⁵
	<i>olivaceus</i>	Peak ¹	26 ⁶	6 (wild) ¹	15 (wild) ¹³	41 ¹⁵
<i>Saimiri</i>	<i>boliviensis</i>	Yes (2 months) ²	~24 ⁷	2.5 (wild) ¹⁰	6 (wild) ⁷	N/A
	<i>oerstedii</i>	Yes (1 week) ²	~12 ⁸	2.5 (wild) ¹⁰	5, 2.5 (wild) ¹⁴	N/A
	<i>sciureus</i>	Yes (1 week) ²	~12 ⁹	N/A	N/A	21 ¹⁶

Sources:

¹ Fragaszy et al. 2004b.² Boinski 1987b.³ Kappeler and Pereira 2003.⁴ Di Bitetti and Janson 2000.⁵ Fedigan and Rose 1995.⁶ Robinson and Janson 1987.⁷ Mitchell, C. L., 1994.⁸ Boinski 1999.⁹ Rowe 1996.¹⁰ Baldwin and Baldwin 1981.¹¹ Patino et al. 1996.¹² Nagle and Denari 1982.¹³ Jack and Fedigan 2004b.¹⁴ Boinski 1994.¹⁵ Hakeem et al. 1996.¹⁶ Harvey et al. 1987.

Atelinae (spider monkeys and woolly monkeys), which generally weigh about four times as much as the average capuchin (see data in Robinson and Janson 1987, Rowe 1996, Kinzey 1997c). Compare, for example, the largest of the New World monkeys, the muriqui (*Brachyteles* spp.), with *Saimiri* and *Cebus*. Female muriquis weigh about 9.5 kg (Rowe 1996) and are 7.5 years of age when they give birth to their first offspring (Strier 1997c). *Saimiri* females weigh on average 700 g and give birth to their first infant at 2.5 years, while *Cebus* females weigh 2.3 kg and are 7–8 years of age when they give birth for the first time (Tables 8.2 and 8.3). Even male *Cebus* show slow maturation rates, with most studies estimating sexual maturity to occur after 7 years of age; and in several species, males do not attain full adult body size until after 10 years of age (Jack and Fedigan 2004a,b). Interestingly, the small size and long life history patterns characteristic of *Cebus* continue to stand out even when we extend comparisons to include the Old World monkeys.

These slow maturation rates of *Cebus* may be related to their extremely long life spans, which average about 41 years in captivity (the record is nearly 55 years; Hakeem et al. 1996). In stark contrast, the smaller *Saimiri* are reported to live only 21 years, and most capuchin-sized (and larger) primates live approximately 30 years (see data presented in Rowe 1996). It is also possible that delayed maturation in *Cebus* is related to their unusually slow postnatal brain growth and motor skill development (see Hartwig 1996). *Cebus* display more postnatal brain growth and development than any of the other platyrrhines, while

Saimiri neonates are more precocial in terms of both brain growth and motor skill development (Hartwig 1995).

GROUP STRUCTURE

Both *Cebus* and *Saimiri* form mixed-sex groups, but the two genera show much diversity in group size and composition (see later section “Cebine Dispersal Patterns”). Although the mean size of *Cebus* groups does not vary greatly across the four better-known species (range = 16.4–21, mean = 18.8), there is considerable variation in adult sex ratios within groups. For example, *C. olivaceus* show the most skewed sex ratios, with approximately one adult male for every two adult females in a group, while *C. albifrons* show the most equitable sex ratios, with 1.08 adult males per female (Table 8.4). The size of *Saimiri* groups is much more variable across species, ranging from 15 to 75 individuals. *S. boliviensis* form the largest groups (mean = 54), while *S. sciureus* display the smallest mean group sizes, at 23 individuals per group. Several researchers have reported *Saimiri* group sizes of up to 300 individuals; however, in all instances, it appeared that these large groups were actually temporary unions of multiple groups (see Sussman 2000 for review). Sex ratios also vary across species, with *S. oerstedii* showing one male per 1.6 adult females and *S. boliviensis* showing a much more skewed ratio, with one male per 2.5 adult females (data are not available for *S. sciureus*) (see Table 8.4). Interestingly, *S. boliviensis* is also the only species of *Saimiri*, indeed of the platyrrhines, reported to form all-male groups; and even within mixed-sex groups, males

Table 8.4 Cebine Social Organization and Social Structure

SPECIES	MEAN GROUP SIZE	MEAN ADULT SEX RATIO (M:F)	DISPERSAL PATTERNS	DOMINANCE
<i>Cebus albifrons</i> ¹	19.8	1.08	Male	Both sexes display linear hierarchies, and males are individually dominant over females; males well-integrated into the group
<i>C. apella</i> ¹	18	0.85	Male	Both sexes display linear hierarchies, and males are individually dominant over females; alpha female may rank below alpha male; subordinate males are often peripheral group members
<i>C. capucinus</i> ¹	16.4	0.71	Male: parallel dispersal is common and lasts through multiple emigration events; female dispersal is rare, but it does occur	Both sexes display linear hierarchies, and males are individually dominant over females; alpha female may rank below alpha male; female coalitions can displace alpha male
<i>C. olivaceus</i> ¹	21	0.53	Male	Both sexes display linear hierarchies, and males are individually dominant over females; alpha female may rank below alpha male
Mean		18.8	0.79	
<i>Saimiri oerstedii</i>	35–65 (41) ²	0.63 (1:1.6) ²	Females disperse prior to first mating season/flexible male philopatry or dispersal ³	Egalitarian; no female dominance hierarchy or coalitions; male hierarchies evident only during mating season ²
<i>S. boliviensis</i> (Peru)	45–75 (54) ²	0.40 (1:2.5) ²	Male: ⁴ parallel dispersal is common and lasts through multiple emigration events ⁴	Females dominant (matrilineal hierarchies and frequent coalitions); both sexes form stable linear dominance hierarchies; ^{5,6} males are peripheral group members
<i>S. sciureus</i> (Suriname)	15–50 (23) ²	NA	Both sexes thought to disperse; female dispersal is flexible (may spend first mating season in natal group) ⁵	Males dominant; both males and females form stable linear hierarchies ⁵

Sources:

¹ All *Cebus* data are from Fragaszy et al. 2004b.² Boinski et al. 2003.³ Boinski 1987a.⁴ Mitchell 1994.⁵ Boinski et al. 2002.⁶ Mitchell 1990.

of this species are generally peripheral and have little to no interaction with group females outside of the mating season (Boinski 1999).

MATING SYSTEMS

Similar to the other platyrrhines, the cebines do not show external cues that signal ovulation or pregnancy like those characteristic of many of the catarrhine primates, making it extremely difficult to discern reproductive from nonreproductive states (Dixon 1983a; see also Chapter 29). In *Cebus*, this lack of obvious fertility signaling, accompanied by the fact that members of the genus show limited reproductive seasonality and engage in frequent nonconceptive copulations (complete with copulatory displays), makes it nearly impossible for observers to discern fertile versus nonfertile matings (e.g., see Manson et al. 1997, Carnegie et al. 2006). Given that *Saimiri* are highly seasonal breeders, with all mating activity being confined to a 2-month period each

year, and that individual females are sexually active for only about a 2-day period throughout these short mating seasons (Boinski 1992) (Table 8.3), determining fertile versus nonfertile matings is not quite as challenging.

Mating behavior in *Cebus*, both conceptive and nonconceptive, is preceded, at least in some species, by elaborate courtship rituals. The most detailed data available to date come from studies of captive *C. apella*. In this species, a female begins the courtship ritual by gazing toward the male of her choice (usually the alpha male), often tilting her head from side to side and raising her eyebrows at him in an attempt to catch his gaze (see Fragaszy et al. 2004b). She slowly decreases the distance between herself and the male and, when she is close enough, reaches out, quickly touches him, and then runs away. Throughout this process, the female continuously rubs her chest and emits soft vocalizations. In these initial stages, her attempts to gain the male's attention seem futile; he appears utterly and completely disinterested. Such solicitation by a female can

go on for hours, but the male eventually relents and begins to reciprocate her movements and vocalizations, adding a mutual gaze and a grin. At this point, the movements of the pair become mirrored in a coordinated dance display. One member of the pair advances, while the other retreats, all the while maintaining their locked gaze. Pirouettes of 180 degrees are added, with the dancer always coming back to face the partner. At this point in the courtship, the participants appear oblivious to what is going on around them. The pair eventually comes together and mating ensues. During copulation, the male emits a loud vocalization that is unique to the mating context; and following ejaculation, the pair remain together, continuing their dance display as if nothing has happened and beginning the process anew.

C. capucinus show a similarly elaborate pattern of courtship and mating, although the eyebrow raising and grinning characteristic of *C. apella* are exchanged for a "duck face," which involves a protrusion of the lips in the direction of the partner (Manson et al. 1997). During their dance displays, *C. capucinus* males and females coordinate their pirouettes and often face away from each other, only to look at their partner either over the shoulder or through the legs. A unique vocalization also accompanies mating in this species, and like the patterns described for *C. apella*, individuals involved in the mating and dance display do not make any attempts to hide their activities. Data on mating in *C. olivaceus* are completely absent from the published literature. The mating behavior and rituals of *C. albifrons*, although not well described, do not appear to be as elaborate as those of either *C. apella* or *C. capucinus*; but data for this species are very limited.

Unlike *Cebus*, *Saimiri* do not show any sort of preparatory behaviors that precede copulation; there are no special vocalizations, displays, or behaviors that indicate readiness or willingness to mate (Mendoza and Mason 1994). That said, *Saimiri* do display one of the most unique reproductive systems reported for nonhuman primates. Prior to and during the short annual mating season, male *S. boliviensis* and *S. oerstedii* undergo dramatic physiological and morphological changes; they gain up to 222 g, a shocking 22% of their body weight (Dumond and Hutchinson 1967) (see Table 8.3; there are no data available for other *Saimiri* species). Males begin accumulating "fat" prior to the start of the annual mating season, and this fattened state is maintained throughout the season, with males reaching their largest size during the same months that the majority of conceptions occur (Schiml et al. 1996). This "seasonal enhancement of male body size" (Boinski 1998:174) results not from the accumulation of fat, as has been reported for rhesus macaques and other mammalian species (see Berkovitch 1992), but from the deposition of water between the skin and muscles, particularly along the shoulders, back, and arms; and it has been likened to the water retention-induced swelling that women often experience before the onset of menstrual cycles (Boinski 1998). This swelling of males

does not occur because they are eating more or doing less. On the contrary, given the high level of reproductive synchrony observed among group females, males are extremely active during the mating season. Male "fattening" is also not related to a restricted seasonal ability to produce sperm. Mendoza et al. (1978) have shown that, although males do experience an increase in testes size and sperm production during the brief mating season, they are fertile year-round. Instead, the fattening appears to be in response to changing hormone levels within individual males, and males that become the fattest are those with the highest testosterone levels (Schiml et al. 1996).

During the nonmating season, there are no discernable size differences among coresident male *Saimiri*; however, with the onset of the mating season, some males become significantly larger than others and one male stands out as the largest. It is this male, the "fattest" male in a group, that is selectively preferred as a mating partner by group females. Indeed, Boinski (1992) reports that the largest male in her study group of *S. oerstedii* participated in over 70% of all observed copulations and the less swollen males were successful in gaining solicitations from females only after the females had been rejected by the largest male. For *S. boliviensis*, the dominant male becomes the most fattened and apparently suppresses the reproductive potential of less swollen subordinate males, although it remains to be determined by exactly what means this suppression occurs (DuMond and Hutchinson 1967). Outside of the mating season, *S. boliviensis* males usually occupy peripheral positions within the group and rarely, if ever, interact with the females that dominate them. However, during the mating season, all males become more central within the group and interact regularly with females (DuMond and Hutchinson 1967). Within groups of *S. oerstedii*, there are no discernable dominance hierarchies either within or between the sexes, even during the mating season. Therefore, rather than dominance status, male enlargement in this species appears to be linked with the length of time a male has spent in a particular group, with long-term residents (>3 years) being the most enlarged and, therefore, the most popular during the mating season (Boinski 1992). At present, it is unclear whether all populations and species of *Saimiri* undergo these seasonal changes; data from additional field sites are needed to address these issues.

The proximate trigger for these morphological changes is still unknown; however, it is possible that males respond to subtle pheromonal or behavioral cues from group females. Male *S. oerstedii* frequently perform genital inspections of females, and this has been interpreted as a means of assessing female reproductive status (Boinski 1987a). Although these inspections occur throughout the year, during the 2 months prior to the commencement of the annual mating season, which is when males begin to fatten, there is a notable increase in the frequency of male coalitionary mobbing of females in order to perform such inspections. Boinski's (1987a) study showed that, at their peak, these

aggressive inspections occur approximately twice per hour and may include up to 16 males. Boinski et al. (2002) even describe one female being wounded during such a mobbing. It is possible that these close inspections trigger the onset of seasonal swelling in males, although additional comparative data of intrasexual hormonal states are needed to test this suggestion. However, the fact that males are at their most swollen at the same time that group females achieve peak fertility (see Boinski 1992; Schiml et al. 1996, 1999) is a good indication that pheromones are at work.

Dominance appears to play a very strong role in the reproductive success of male *Cebus*. In all three species for which data on wild groups are available, a significant link between male dominance rank and reproductive success has been found, with alpha males siring the majority of infants born (*C. apella*, Escobar-Páramo 2000; *C. capucinus*, Jack and Fedigan 2003, 2006; *C. olivaceus*, Valderrama et al. 2000a). Given the rather divergent mating systems seen across the genus, the consistency of the positive correlation between male dominance rank and reproductive success is surprising. Although a distinctive male dominance hierarchy is discernable in *C. capucinus*, male/male intragroup competition for access to mates has not been documented. The alpha male does not monopolize matings, nor does he appear to be the exclusive target of female choice (Fedigan 1993); and all males within the group experience some degree of mating success (e.g., Rose 1998). However, paternity analysis in the Santa Rosa study groups has demonstrated that alpha males sire the majority of infants born into their groups (Jack and Fedigan 2003, 2006). Consequently, regardless of the apparently egalitarian mating system of this species, reproduction is not shared among group males (see Jack and Fedigan 2006). A recent study of *C. capucinus* by Carnegie et al. (2006) has shown that matings between females and alpha males occur during fertile periods, while those between females and subordinate males tend to occur during nonfertile times (when females are pregnant, lactating, or in the postovulatory phase). However, it is still unclear which sex is responsible for the timing of fertile matings, that is, whether females select to mate with alpha males during their fertile times or if a more subtle form of mating competition occurs and alpha males somehow exclude subordinates from mating with fertile females.

The two other well-studied species of *Cebus* (*C. apella* and *C. olivaceus*) show tense relationships among group males, and although both species reside in multimale groups, they are described as being functionally unimale, with the dominant male monopolizing matings and subordinate males being peripheral group members (e.g., *C. apella*, Janson 1985b, 1986; *C. olivaceus*, Robinson 1988a, O'Brien 1991). Reproductive success within groups of these two species largely reflects the observed social patterns, with alpha males monopolizing reproductive success (*C. apella*, Escobar-Páramo 2000; *C. olivaceus*, Valderrama et al. 2000a), although, at least for *C. apella*, beta males also sire

offspring, particularly with the daughters of alpha males (Escobar-Páramo 2000).

CEBINE DISPERSAL PATTERNS: TOWARD AN EXPLANATION OF VARIABLE SOCIAL STRUCTURE

The dispersal of one or both sexes from the birth group is a pattern common to all social mammals and birds, and many species show a bias toward the dispersal of one sex over the other (Greenwood 1980). The majority of Old World cercopithecines and prosimians are characterized by male-biased dispersal and female *philopatry* (the tendency to remain in the birth group for life), while New World monkeys and apes tend toward bisexual dispersal (e.g., *Alouatta* and *Gorilla*) or female-biased dispersal (e.g., *Ateles* and *Pan*) (see Pusey and Packer 1987 for review, Strier 1999). Dispersal is said to be among "the most important life history traits involved in both species persistence and evolution" (Clobert et al. 2001); however, despite its importance and the fact that it is one of the most studied phenomena, it remains among the most poorly understood issues in ecology and evolutionary biology (Clobert et al. 2001). Without a doubt, dispersal patterns have a profound influence on the type and nature of social relationships within groups. For example, in species characterized by male-biased dispersal, females within groups are related, most often show close bonds, and regularly form matrilineally based dominance hierarchies (e.g., *Macaca mulatta*, *M. fuscata*, and *Papio cynocephalus*). Within female philopatric groups, males are generally considered to be unrelated and their social relationships are usually characterized by very low levels of affiliation and cooperation. In general, the opposite pattern of social relationships is observed when males are philopatric (e.g., chimpanzees and muriquis, although bonobos are an exception to this pattern), while those species characterized by bisexual dispersal most often show much looser bonds among same-sexed individuals and closer bonds between the sexes (e.g., gorillas) (for reviews see Pusey and Packer 1987, van Hooff 2000).

Unlike most platyrrhine species, *Cebus* are characterized by female philopatry and male dispersal from the birth group; in this respect, they more closely resemble Old World monkeys. In general, *Cebus* are considered female-bonded (Wrangham 1980) or resident nepotistic (Sterck et al. 1997) in that (1) they exhibit female-biased philopatry and male dispersal, (2) affiliative bonds among females are generally stronger than they are between the sexes or among males, (3) females develop dominance hierarchies, and (4) females appear to be responsible for the direction of group movement (Fragaszy et al. 2004b; but see Phillips and Newlon 2000 on *C. albifrons trinitatis*). In addition, field studies are shedding light on the importance of kinship in the formation of female/female relationships and, although it may not be as decisive a factor as observed among the Old

World cercopithecines, this does appear to play a prominent role in at least some species of *Cebus* (*C. capucinus*, Rose 1998, Perry 1996; *C. olivaceus*, O'Brien and Robinson 1991). In terms of relationships between the sexes, males are generally individually dominant over adult females for all species; however, at least for the three better-studied species (*C. apella*, *C. capucinus*, and *C. olivaceus*), an alpha female will often rank directly below the alpha male and dominate individual subordinate males within the group (Fragaszy et al. 2004b). In addition, females will often form coalitions that enable them to displace even the alpha male from feeding trees and, at least for *C. capucinus*, females tend to direct more threats toward males than they receive from them (Perry 1997, Rose 1998). Overall, this results in somewhat egalitarian relationships between males and females; and across the genus, these relationships are best characterized as being affiliative in nature, with little physical aggression being exchanged between the sexes.

Throughout the genus, social relationships among group members are maintained through the exchange of frequent grooming, the maintenance of proximity, and the frequent formation of coalitions with preferred partners (Fragaszy et al. 2004b). Although social relationships among females and between the sexes across the better-studied *Cebus* species are remarkably consistent, male capuchins display extensive variation in their relationships with one another. Male/male relationships within the genus range from despotic (*C. apella*, Janson 1986; *C. capucinus*, Perry 1998b; *C. olivaceus*, Robinson 1988b) to highly affiliative and cooperative (*C. albifrons*, Janson 1986; *C. capucinus*, Jack 2003a), and, at least for *C. apella* and *C. capucinus*, which have been studied the most extensively and at multiple sites, this variability in male/male relationships exists both within and among species. For example, the first published accounts of male relationships in *C. apella* in Peru reported that alpha males directed high rates of aggression toward subordinate males, which remained on the periphery of the group, avoiding interactions with the alpha male and resident females (Janson 1985a 1986). However, additional studies on *C. apella* at multiple sites have yielded a more diverse view of male relationships within this species. In Colombia (Izawa 1980, 1994), Brazil (Lynch et al. 2002), and Suriname (Kauffman et al. 2004), males are reported to display low rates of aggression and frequently interact affiliatively, while in Argentina (Janson 1998a and personal communication), male *C. apella* exhibit greater levels of cooperation in resource defense, although relationships between dominants and subordinates are still described as agonistic.

Similarly, male relationships in *C. capucinus* have been reported as highly variable, and this variability occurs not only across study sites but also among groups within the same study population (e.g., Santa Rosa National Park in Costa Rica, where studies have been ongoing since 1983; see Jack 2003a). In terms of access to mates and resources, relationships among males are fairly egalitarian, with little

aggression being exchanged among group males. Although a distinct alpha male is discernable within groups, it is the extent to which he asserts his dominance that appears to be most variable. For example, some alpha males actively, and often aggressively, disrupt affiliative interactions among subordinate coresident males and spend the majority of their time affiliating with group females (Perry 1998a,b), while other alphas form close affiliative relationships with subordinates and, in some groups, spend more time interacting with them than with group females (Jack 2003a).

This diversity in male relationships across *Cebus* likely reflects the behavioral plasticity characteristic of the genus (see Fragaszy et al. 1990), and within species, male relationships are apt to change in response to ecological and/or social pressures (e.g., Janson 1998a, Di Bitetti and Janson 2001a). Ecological factors appear to play an important role in determining male/male relationships in *C. apella*, which has now been studied in five countries throughout South America (Argentina, Brazil, Colombia, Peru, and most recently Suriname). Janson (1986) suggests that it is the distribution of food resources and a male's ability to monopolize access to them that most profoundly influence primate mating systems, which in turn dictate the types of social relationships among group males. Janson (1986) argues that if a single male is able to dominate individual access to resources, it is likely that females will choose to mate with him to ensure resource access for themselves and their infants. Under these circumstances, the mating system essentially becomes unimale. Such a skewed mating system results in rather tense male/male relationships, with males tending to be less inclined to cooperate in group and resource defense when there is little reward for their assistance (i.e., little mating activity) (see van Hooff 2000). If, on the other hand, resources are distributed in such a way that they cannot be monopolized by a single individual (e.g., they occur in large patches), females need not choose to mate exclusively with the alpha male and a more egalitarian mating system may result. This mating system may lead to increased male cooperation in resource defense (Janson 1984), although it may also result in increased within-group mating competition and does not necessarily trigger affiliative relationships among group males.

Such differences in ecological factors, namely the defensibility of food resources, do not, however, explain the intergroup variability in relationships among coresident male *C. capucinus* that is reported to occur within the same study populations (see Jack 2003a; S. Perry, personal communication). It appears that within groups of *C. capucinus*, male familiarity, and perhaps kinship, best explains the observed variability (Jack 2003a). Although *C. capucinus*, like all *Cebus* species, is characterized by the emigration of males from their birth group, high rates of parallel dispersal can, in the absence of philopatry, promote the retention of kinship among group males (van Hooff 2000). Parallel dispersal can occur through the coordinated emigration of male siblings

or the movement of males toward groups that contain familiar, previously dispersed males. This type of coordinated male dispersal has been reported for several primate species, although in most species it appears to be limited to particular life phases and to be most common among immature males (see Jack 2003b, Schoof et al. 2009). However, studies of *C. capucinus* in Santa Rosa National Park, Costa Rica, found that parallel dispersal occurs at extremely high levels (67%–80% of all emigrations depending on male age class), lasts through multiple dispersal events, and persists at high rates even among adult males (Jack and Fedigan 2004a,b). In addition, analysis of male/male interactions in this species has shown that familiar males do display more affiliative relationships (Jack 2003a), and Janson (personal communication) suspects that male familiarity and/or relatedness may well account for the more cooperative relationships he has observed among male *C. apella* in Argentina. *C. apella* groups in Argentina contain more males than those Janson first studied in Peru, which may enable parallel dispersal to occur more readily. Relatedness among group males in both *C. apella* in Argentina and *C. capucinus* in Costa Rica, and perhaps in *C. olivaceus* (although very little is known about the dispersal patterns of this species), may explain the high degree of cooperation among group males in the face of the unimale reproductive system each of these species exhibits (see earlier section "Mating Systems"). We eagerly await genetic analyses of male kinship within groups so that these predictions can be tested.

Despite the remarkable similarity that *Saimiri* species display in terms of morphology and general habitat preference, the genus shows an even greater diversity in social relationships than we see in *Cebus*. However, across the three species for which sufficient data are available (*S. oerstedii*, *S. boliviensis*, and *S. sciureus*), it is the social relationships among group females and between males and females that are extremely variable, while relationships among group males are surprisingly consistent (Table 8.4). Boinski, who has studied this genus extensively over the past two decades, claims that "squirrel monkeys arguably exhibit the most geographically variable social organization of any set of closely related primate populations" (1998:179). The variability that we see across the genus appears to directly reflect the extremely divergent dispersal patterns observed among the species (see Boinski et al. 2005a,b; Boinski 2005), which are likely determined by the nature and distribution of resources each species exploits. Interestingly, the formation and maintenance of social bonds throughout this genus are not based on grooming interactions, as is the case for many nonhuman primates. In fact, *Saimiri* are among the few primate species where social grooming is almost completely absent. Instead, social relationships are based on proximity patterns, tolerance around feeding sources, the frequent exchange of vocalizations, and the formation of alliances in some species (see Sussman 2000 for review; Boinski 1999).

S. oerstedii in Costa Rica are characterized by female emigration from the birth group (Boinski and Mitchell 1994) and a flexible pattern of male philopatry. While females typically disperse as juveniles before their first mating season, secondary dispersal is not uncommon and appears to be linked to the survivorship of offspring. In one long-term study, all females whose offspring died transferred to a new group before the start of the next mating season (see Boinski et al. 2005a). A natal male will generally remain in his birth group until he reaches sexual maturity (4–5 years), after which he will either take up one of the few reproductive positions within the group or disperse with members of his age cohort and attempt to take over breeding positions in another group (Boinski 1998). No matter which pattern is followed, it is thought that resident males of this species are related as a result of parallel dispersal. This dispersal pattern leads to strong affiliative bonds among group males, while female bonds are described as weak (Boinski 1999, Boinski and Mitchell 1994) and relationships between males and females are described as being extremely egalitarian, with neither males nor females being dominant over the other (Boinski 1987a, 1988a). With the exception of the 2-month period prior to the mating season when males are observed to form coalitions and frequently to mob females to perform genital inspections (see earlier section "Mating Systems"), aggression within and between the sexes very rarely occurs. Even intergroup interactions are described as neutral, although avoidance is generally practiced (Boinski, 1987a, 1988a).

In contrast, *S. boliviensis* in Peru display female philopatry; and accordingly, although perhaps more so than any other species of platyrrhine primate, females form tight-knit matrilineal relationships that cooperate in resource acquisition and defense (Mitchell, C. L., 1990, 1994; Mitchell et al. 1991). Intragroup resource competition is described as occurring at moderate levels within this species, and it occurs both among and between the sexes (Boinski 1999). Interestingly, despite the fact that this is the most sexually dimorphic of the *Saimiri* species, with males being 24% larger than females (Table 8.2), females form stable linear dominance hierarchies, dominate males, and aggressively force them to occupy peripheral positions within the group (Mitchell, C. L., 1990, 1994). Within these peripheral subgroups, males also form stable linear dominance hierarchies and, although social aggression is described as common (Boinski 1999), affiliative coalitions that are often maintained through multiple emigrations (i.e., parallel dispersal) may work to ensure kinship among group males (Mitchell, C. L., 1994). *S. boliviensis* males emigrate with other natal males of the same age and will typically join an all-male band or bachelor group before attempting to infiltrate a new group. More often than not, males enter a new group which contains familiar males from their natal cohort (Boinski et al. 2005a). *S. boliviensis* groups have home ranges that overlap extensively, and intergroup interactions are nonaggressive; in areas where fruit patch size allows, it

is not uncommon to see groups foraging together (Mitchell 1990).

S. sciureus presents yet another configuration of dispersal patterns, social interactions, and dominance structures for the genus. Both male and female *S. sciureus* disperse from their birth group (Boinski et al. 2005a). Female natal emigration may occur before or after the first mating season and appears to be linked to relative access to food and overall food abundance (Boinski 2005). The dispersal of natal male *S. sciureus*, on the other hand, usually occurs well before sexual maturity. However, those males who delay natal dispersal are often forcibly evicted as they approach sexual maturity (Boinski et al. 2005a). *S. sciureus* display the highest level of intragroup aggression reported among the three *Saimiri* species. The majority of this aggression occurs within the context of resource acquisition, and wounding of females and immatures is common, something which is rarely seen in the other two species (Boinski et al. 2002). Overall, *S. sciureus* is best described as being male-dominant; and although both males and females form stable linear dominance hierarchies, males are reported to be more closely bonded in that they form more frequent cooperative coalitions with moderate to close affiliative relationships (Boinski 1999). However, the majority of males spend their adult life as solitary or peripheral individuals, and very few achieve secure resident status within a group (Boinski et al. 2005a). Unlike the other two species of *Saimiri*, which do not display tense interactions with neighboring groups, *S. sciureus* in Suriname are described as territorial. Their home ranges show minimal overlap with other groups, and intergroup interactions are described as highly agonistic (Boinski 1999).

In an attempt to explain the variable patterns of female relationships seen across this genus, Boinski et al. (2002) provide an extensive examination of the detailed ecological data available for the three species of *Saimiri*. Following Janson (1986) and his explanation of variable relationships among *Cebus* males, Boinski et al. (2002) suggest that the extreme variability in dispersal patterns and the corresponding social relationships among group members (at least among group females) that characterize *Saimiri* are largely attributed to ecological factors associated with the defensibility of food resources, namely fruit patch size and abundance. As mentioned, *Saimiri* are classified as insectivore–frugivores and insects form the bulk of their diets, with all species spending an average of 75%–80% of their time foraging for insects (Terborgh 1983, Boinski 1988a). The distribution of arthropods does not enable a single individual, or even groups of individuals, to effectively monopolize the food supply; therefore, direct competition (*contest competition*) for this resource is absent (Boinski 1988a, Mitchell 1990). However, fruit is also a key resource exploited by *Saimiri*; and even though the habitats of the three well-known species are quite uniform in terms of relative abundance and distribution of

arthropods, these habitats do display extensive variability in fruit production.

A comparison of fruit patch size and abundance demonstrates that, overall, Peruvian forests have the highest levels of fruit abundance and the lowest fluctuations in seasonal availability of fruit, followed by Costa Rican forests, while Surinamese forests show the lowest abundance and greatest seasonal fluctuations (Boinski et al. 2002). Hence, it is not surprising that in Peruvian forests, where food patches are too large to be effectively monopolized by a single individual, females cooperate with kin to defend access to these resources and exclude males. Cooperation is necessary because males are larger and, therefore, it is beneficial for females to remain philopatric and cooperate with their kin to control access to resources (Boinski et al. 2002; see also Sterck et al. 1997). In Costa Rica, where fruit is distributed in such a way that it cannot be monopolized by either a group or a single individual (it can be eaten on the spot on a first-come, first-served basis), it is not advantageous for females to remain in their birth group, a condition which most often leads to male philopatry. In the Surinamese forests, fruit patches are small and in relatively low abundance, making an individual patch easily monopolized by single individuals and of great benefit for those that can gain access to them, namely dominants. This type of distribution leads to very strong contest competition; therefore, it makes sense for a female to disperse so that she is not directly competing with kin for access to necessary resources. According to Boinski et al. (2002), this type of situation will not promote stable coalitions among individuals because cheating (i.e., reneging on sharing resources with a coalition partner) would provide great benefits to dominant individuals.

Boinski and Cropp (1999) state that, across the three species, relationships among male squirrel monkeys are rather consistent—males show affiliative bonds—while female/female bonds vary from strong to weak and male/female relationships also vary from species to species. They provide a very good example of how even slight differences in ecological factors (e.g., quality, size, and defensibility of food patches) can have profound effects on primate social structure and how these factors influence the variable nature of female/female and female/male relationships across the genus. They do not, however, offer an explanation for the consistency of male/male relationships in the face of the vast ecological variability that can be seen across the genus. Familiarity and/or relatedness among group males likely explains the relative consistency in male/male relationships across the genus *Saimiri*. It seems likely that in all three species males within groups maintain some degree of relatedness to one another. In *S. oerstedii*, males either are philopatric or disperse together in cohorts, which also appears to be the case for male dispersers in *S. sciureus* and *S. boliviensis*. In *S. boliviensis*, where male emigration is the norm, relatedness among

group males also appears to be maintained through parallel dispersal. C. L. Mitchell (1994) reports that males form dispersal alliances whose composition often remains constant over multiple emigration events, and this may act to ensure the relatedness of males in the face of dispersal. These data show that, regardless of ecological pressures and female dispersal patterns, males in the genus appear to have evolved a mechanism for retaining residence with their kin, regardless of dispersal patterns. A recent meta-analysis of parallel dispersal by male nonhuman primates found that this behavior may have evolved in species where it is important for males to retain coalition partners in the face of male dispersal (Schoof et al. 2009).

Additional comparative studies are needed to further our understanding of ecological pressures on social relationships, mating systems, and dispersal patterns. In addition, genetic data on the relatedness of group members (both males and females) and more detailed reports on dispersal patterns and the fates of dispersing individuals in other species are required in order to attain a more complete overview of the dynamics and interactions that these processes have on primate behavior.

Species included in this chapter are shown in Color Plates 9, 10, and 17 (*Cebus capucinus*, *Cebus apella*, and *Saimiri sciureus*).

9

Sakis, Uakaris, and Titi Monkeys

Behavioral Diversity in a Radiation of Primate Seed Predators

Marilyn A. Norconk

1. What is seed predation, and how do seeds provide both benefits and costs to sakis, bearded sakis, and uakaris?
2. How do pitheciines differ in their social group and ranging patterns using body size and group size as relevant variables?
3. How is male affiliation manifested in pitheciines and how does it compare with woolly spider monkeys, chimpanzees, and bonobos?"

INTRODUCTION

The pitheciines are a cohesive group of New World monkeys phylogenetically and in terms of diet but exhibit a range of variation in group size, use of space, and social dynamics. At one end of a continuum that ranges from small to large group sizes, titi monkeys (*Callicebus* spp.) form cohesive, pair-bonded groups that in many ways represent the "classic monogamous" pattern (Fuentes 1999b, van Schaik and Kappeler 2003) (Table 9.1). Pairs are generally territorial, adults are monomorphic in body size and color. They exhibit social and physiological mechanisms that promote and reinforce attachment between mates, and males are strongly paternalistic (Mason 1968, 1971; Fragaszy et al. 1982; Kinzey 1981; Menzel 1986; Mendoza and Mason 1986a,b; Mason and Mendoza 1998; Schradin et al. 2003; Bales et al. 2007).

Bearded sakis (*Chiropotes* spp.) and uakaris (*Cacajao* spp.) are at the other end of the group size continuum. They form large, more loosely structured groups that may fission into smaller feeding parties (Ayres 1986; Norconk and Kinzey 1994; Kinzey and Cunningham 1994; Defler 1999a, 2003a; Veiga 2006; Bowler et al., 2009). Groups travel through large home ranges and day ranges are as long as those of any platyrrhine (Ayres 1981, 1986; Norconk and Kinzey 1994; Aquino 1998; Boubli 1999; Defler 1999a; Peetz 2001; Barnett et al. 2002). Males do not take an active part in infant care. Bearded saki and uakari males are generally larger than females (Table 9.2) and exhibit sex-specific characteristics of robusticity such as enlarged temporal muscles (Figs 9.1 and 9.2). Both male and female bearded sakis exhibit well-developed beards upon sexual maturity and colorful, relatively large external genitalia (pink scrotum